Catalogue of American Amphibians and Reptiles.

Ernst, C.H. 2002. *Storeria occipitomaculata.*

Storeria occipitomaculata (Storer)
Red-bellied Snake

Coluber leberis Linnaeus 1758:216. Type locality, "Habitat in Canada." Holotype, a male; originally either collected by Kalm or in Kalm's collection. See **Remarks**.

Coluber occipito-maculatus Storer 1839:230. Type locality, "Amherst," Hampshire County, Massachusetts. Holotype, collected by Professor Adams, date not reported; specimen apparently lost.

Coluber venustus Hallowell 1847:278. Type locality, "Michigan, near Copper Harbor [Keweenaw County], Lake Superior ... between stones upon the border of the lake..." Holotype, Academy of Natural Sciences of Philadelphia (ANSP) 5907, adult, sex undetermined, collected by T.F. Moss, Esq. in 1847 (examined by author).

Tropidonotus occipito-maculatus: Holbrook 1842:55.

Storeria occipito-maculata: Baird and Girard 1853:137.

Ischnognathus dekayi, varieté B: Duméril, Bibron, and Duméril 1854:509.

Ischnognathus occipitomaculatus: Günther 1858:81.

Storeria occipitomaculata: Yarrow 1883:129. First use of current combination.

• **CONTENT.** Three subspecies are recognized: *Storeria o. occipitomaculata, S. o. obscura*, and *S. o. pahasapae* (see **Remarks**).

• **DEFINITION.** *Storeria occipitomaculata* is a small snake with a maximum TL of 40.6 cm (maximum female TL = 40.6 cm; maximum male TL = 35.9 cm), but most individuals are 21–27 cm long. Neonates are 6.1–10.9 cm long. The pitless, keeled body scales lie in 15 (16–17) anterior rows, 15 (13–17) midbody rows, and 15 (13–15) rows near the tail. Ventrals number 107–136, subcaudals 34–63, and the cloacal scute (= anal plate) is divided. Males have 107–134 ($\bar{x}$ = 120) ventrals, 42–63 ($\bar{x}$ = 50) subcaudals, and tail lengths 20–27% ($\bar{x}$ = 24.5) of TL; females have 111–136 ($\bar{x}$ = 124) ventrals, 34–56 ($\bar{x}$ = 43) subcaudals, and tail lengths 17–24% ($\bar{x}$ = 21.5) of TL.

Dorsal head scales consist of a rostral scale, 2 internasals, 2 prefrontals, a medial frontal, 2 supraoculars, and 2 parietals. Scales on the side of the head are 2 nasals, 2 (rarely 1) preoculars, 2 (1–3) postoculars, 1 + 2 (1–3) temporals, 6 (5–8) supralabials, and 7 (5–8) infralabials. No loreal scale is present. A small mental scale, 2 long anterior chin shields, and 2 shorter, posteriorly separated, posterior chin shields occur on the underside of the head.

Dorsal body color varies from pale to dark brown to olive-black or gray, and extends onto the venter. The venter is red, orangish, yellow, or tan. Three small, pale light blotches are present on the neck. The dorsum may have a narrow, pale vertebral stripe or narrow dark longitudinal stripes. The chin and throat are usually whitish, and the lower jaw may be dark-spotted. The pale neck blotches sometimes fuse to form a complete ring. Any of the the pale markings may be absent. A pale spot is usually present on the 5th supralabial scale.

The distinct pale (gray) and dark (brown or olive-black) color morphs are found in varying proportions in eastern populations with no color intergradation between them. Because these color morphs are members of a common gene pool, three possibilities exist for this polymorphism: (1) it is a selectively neutral trait and color proportions vary due to genetic drift; (2) balanced selection for the alleles involved in color polymorphism; or (3) balanced selection for one or more genes that are linked to the color genes (Grudzien and Owens 1991). More data are needed on the proportions of the two color morphs over the entire geographic range to determine which possibility is in play.



FIGURE 1. *Storeria occipitomaculata occiptomaculata*, Kentucky (photograph by Roger W. Barbour).



FIGURE 2. *Storeria occipitomaculata obscura*, Michigan (photograph by Peter G. May).

The short, single hemipenis has a medial sulcus spermaticus, which extends laterally from the posterior base and then straight to the apex, a flattened distal end, and 5 lateral spines, which are larger near the base, but no very enlarged basal spines.

Each maxilla has 14–15 teeth of equal length, although the posteriormost 2 to 3 are thicker than the rest; the dentary bears 16–18 teeth; and the palato-pterygoid has 30–35 teeth.

The karyotype consists of 36 chromosomes (34 macrochromosomes, 2 microchromosomes), females are ZW, males are ZZ (Hardy 1971).

• **DESCRIPTIONS. General descriptions** are in Boulenger (1893), Loennberg (1894), Cope (1900), Hurter (1911), Wright and Bishop (1927), Bishop and Alexander (1927), Haltom (1931), Kelly (1936), Conant and Bridges (1939), Trapido (1944), Conant (1957), Wright and Wright (1957), Smith (1961), Anderson (1965), Behler and King (1979), Smith and Brodie (1982), Gilhen (1984), Stebbins (1985), Ernst and Barbour (1989), Burgason (1992, 1999), Palmer and Braswell (1995), Harding (1997), Conant and Collins (1998), and Ernst and Ernst (2003). The Duvernoy's gland was described by Taub (1967).

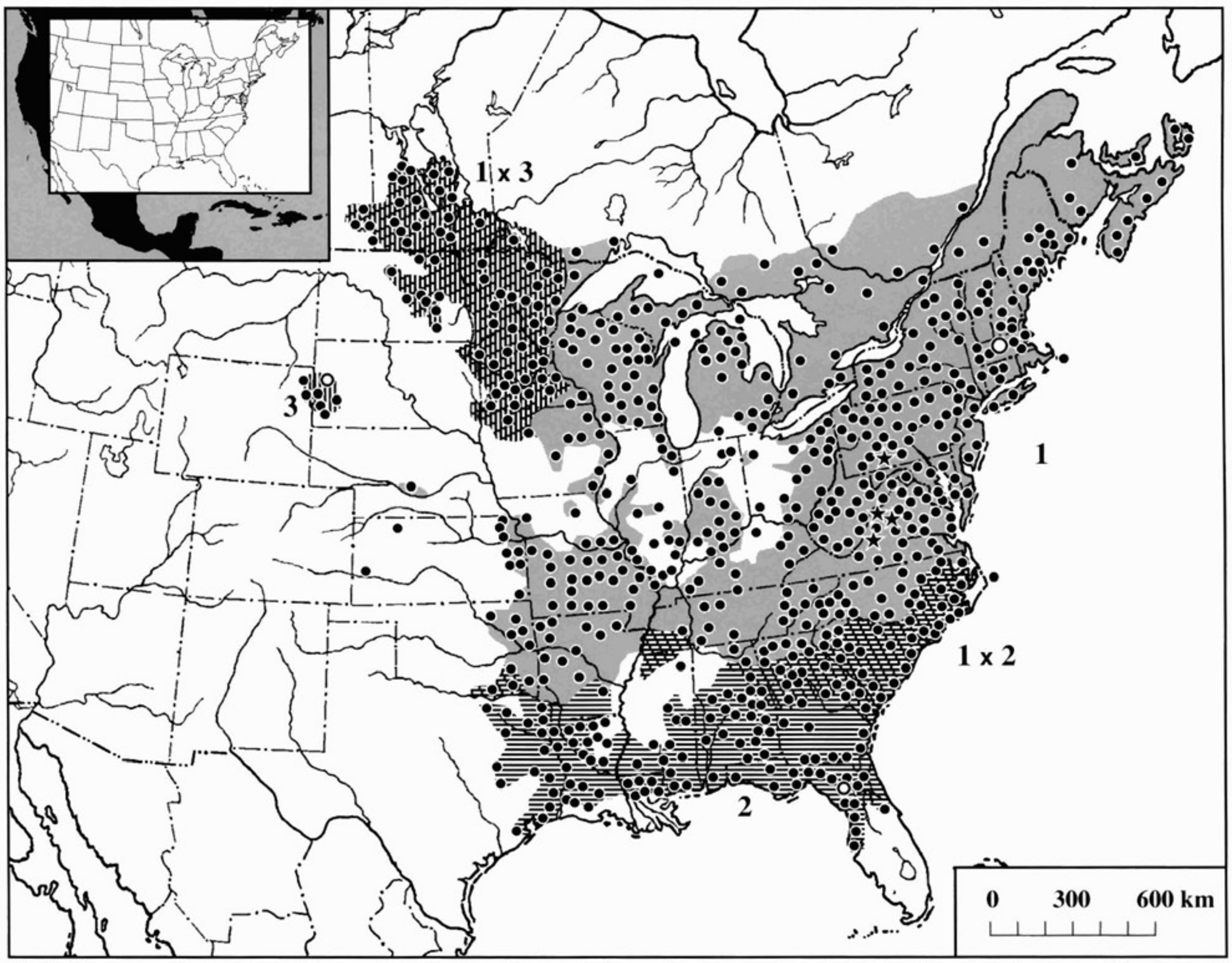
• **ILLUSTRATIONS. Color drawings or photographs** of whole individuals are found in Schmidt and Inger (1957),

Barbour (1971), Snyder (1972), Behler and King (1979), Martof et al. (1980), Ashton and Ashton (1981), Preston (1982), Smith and Brodie (1982), Jackson (1983), Tennant (1985, 1997, 1998), Green and Pauley (1987), Ernst and Barbour (1989), Sievert and Sievert (1989), Christansen and Bailey (1990), Shaffer (1991), Allen (1992), Burgason (1992), Holman et al. (1993, 1999), Klemens (1993), Mitchell (1994), Oldfield and Moriarty (1994), Palmer and Braswell (1995), Harding (1997), Conant and Collins (1998), Hunter et al. (1999), Johnson (2000), Tennant and Bartlett (2000), and Ernst and Ernst (2003). **Black and white drawings or photographs** are in Hallowell (1847), Bishop and Alexander (1927), Haltom (1931), Trapido (1937, 1944), Conant and Bridges (1939), Ditmars (1935, 1939), Schmidt and Davis (1941), Breckenridge (1944), McCauley (1945), Conant (1957), Wright and Wright (1957), Anderson (1965), Wheeler and Wheeler (1966), Cook (1967), Huheey and Stupka (1967), Froom (1972), Mount (1975), DeGraaf and Rudis (1983), Gilhen (1984), Baxter and Stone (1985), Ernst and Barbour (1989), Burgason (1992), Hunter et al. (1992, 1999), Collins (1993), and Boundy (1997).

The **head and neck** are illustrated in black and white drawings or photographs or color photographs in Cope (1900), Wright and Bishop (1927), Haltom (1931), Schmidt and Davis (1941), Trapido (1944), Wright and Wright (1957), Logier (1958), Smith (1963), Linzey (1979), Rossman and Erwin (1980), Linzey and Clifford (1981), Smith and Brodie (1982), Cook (1984), Stebbins (1985), Dundee and Rossman (1989), Brothers (1992), Palmer and Braswell (1995), Powell et al. (1998), and Amaral (1999). Other illustrations are as follows: **body stripes or scales** (Cope 1900, Haltom 1931, Trapido 1937, Wright and Wright 1957, Brothers 1992), **venter** (Cope 1900, Haltom 1931, Wright and Wright 1957, Brothers 1992), **slough** (Wright and Wright 1957), **teeth and teeth-bearing bones** (Rossman and Myer 1990, Amaral 1999), **young** (Bishop and Alexander 1927), **lip-curling behavior** (Amaral 1999), and **habitat** (Klemens 1993). A graph showing the **annual activity cycle** is in Gibbons and Semlitsch (1987).

• **DISTRIBUTION.** *Storeria occipitomaculata* is found from Nova Scotia west to southeastern Saskatchewan, and south to central Florida and the Gulf Coast west to eastern Texas. Relictual populations occur in the Black Hills of South Dakota and adjacent Wyoming, Nebraska (Peyton 1989), and western Kansas, although Collins (1993) suggested that the latter records are not valid.

Publications discussing distribution include Weber (1936), Creaser (1944), Trapido (1944), Wheeler (1947), Dundee (1948), Hatt et al. (1948), Triplehorn (1948), Logier (1958), Cliburn (1959), Fishbeck and Underhill (1959), Cook and Nero (1961), Logier and Toner (1961), Long (1961), Smith (1963), Cook (1967), Ernst (1974), Erwin and Rossman (1975), Lardie (1976), Williamson and Moulis (1979), Rossman and Erwin (1980), McCoy (1982), Hjertaas (1983), Dixon (1987), Hruska (1989), Lamb et al. (1998), and Platt et al. (1999).



MAP. Distribution of *Storeria occipitomaculata*. Type localities are designated by circles, other selected locality records by dots, and fossil records by stars. Records in western Kansas were not considered valid by Collins (1993), although Peyton (1989) speculated that those populations may be extant.

Various distribution maps are presented in Breckenridge (1944), McCauley (1945), Wright and Wright (1957), Logier (1958), Anderson (1965), Wheeler and Wheeler (1966), Webb (1970), Raun and Gehlbach (1972), Ernst (1974), Behler and King (1979), Martof et al. (1980), Rossman and Erwin (1980), Ashton and Ashton (1981), Lindsey and Clifford (1981), Preston (1982), Smith and Brodie (1982), DeGraaf and Rudis (1983), Cook (1984), Gilhen (1984), Baxter and Stone (1985), Stebbins (1985), Tobey (1985), Dixon (1987), Green and Pauley (1987), Ernst and Barbour (1989), Tennant (1984, 1985, 1997, 1998), Shaffer (1991), Burgason (1992, 1999), Collins (1993), Klemens (1993), Mitchell (1994), Oldfield and Moriarty (1994), Palmer and Braswell (1995), Harding (1997), Conant and Collins (1998), and Ernst and Ernst (2003).

• **FOSSIL RECORD.** Fossils attributed to *Storeria occipitomaculata* have been found in Pleistocene Rancholabrean II deposits at the New Paris Site, Unit I (approximately 11,300 B.P.), Bedford County, Pennsylvania (Lynch 1966; Guilday et al. 1964; Fay 1988; Holman 1995, 2000); at Clark's Cave (11,000 B.P.), Bath County, Virginia (Holman 1987, 1995, 2000; Fay 1988); and at Natural Chimney's, Augusta County, Virginia (Guilday 1962; Lundelius et al. 1983; Holman 1987, 1995, 2000; Fay 1988). Another Rancholabrean II fossil, tentively assigned to *S. occipitimaculata*, is known from Straight Canyon Fissure, Highland County, Virginia (Fay 1984; Holman 1995, 2000). Other fossils identified only to the genus *Storeria* may also be of this species (Holman 2000).

• **PERTINENT LITERATURE. General accounts** are in Surface (1906), Hurter (1911), Bishop and Alexander (1927), Haltom (1931), Ditmars (1935, 1936, 1939), Trapido (1937), Conant and Bridges (1939), Carr (1940), Schmidt and Davis (1941), Breckenridge (1944), McCauley (1945), Conant (1951), Cook (1954), Wright and Wright (1957), Logier (1958), Smith (1961), Anderson (1965), Wheeler and Wheeler (1966), Huheey and Stupka (1967), Barbour (1971), Froom (1972), Minton (1972), Snyder (1972), Mount (1975), Cockington (1978), Behler and King (1979), Linzey (1979), Martof et al. (1980), Ashton and Ashton (1981), Linzey and Clifford (1981), Pewtress (1981), Vogt (1981), Preston (1982), DeGraaf and Rudis (1983), Jackson (1983), Gilhen (1984), Tennant (1984, 1985, 1997, 1998), Baxter amd Stone (1985), Green and Pauley (1987), Dundee and Rossman (1989), Ernst and Barbour (1989), Sievert and Sievert (1989), Christiansen and Bailey (1990), Gibbons and Semlitsch (1991), Allen (1992), Brothers (1992), Burgason (1992, 1999), Hunter et al. (1992, 1999), Collins (1993), Holman et al. (1993, 1999), Klemens (1993), Mitchell (1994), Oldfield and Moriarty (1994), Palmer and Braswell (1995), Ernst et al. 1997, Harding (1997), Fitch (1999), Johnson (2000), Tennant and Bartlett (2000), and Ernst and Ernst (2003).

Other papers, listed by topics, include: **systematics and taxonomy** (Schmidt 1953, Smith and Huheey 1960, Marx and Rabb 1972, Ernst 1974, Erwin and Rossman 1975, Rossman and Erwin 1980), **common names** (Banks et al. 1987, Collins 1990, Frank and Ramus 1995), **type locality** (Schmidt 1954), **zoogeography** (Hatt et al. 1948; Bleakney 1958; Holman 1995, 2000), **karyotype** (Hardy 1971, Hubble 1971), **functional morphology** (Amaral 1999), **lungs** (Wallach 1998), **Duvernoy's gland and venom potential** (Taub 1966, 1967; McKinistry 1983), **renal function** (Bordley and Richards 1933), **seminal receptacles** (Fox 1956), **sexual dimorphism** (Clark 1967, Fitch 1981), **length** (Boundy 1995), **reproduction** (Hallowell 1849; Ruthven 1906; Hahn 1908; Langlois 1924; Myers 1924; Weber 1928; Blanchard 1937; Trapido 1940; Cohen 1948; Loomis and Jones 1948; Oliver 1955; Fox 1956; Hedrick and Holmes 1956; Denman and Lapper 1964; Nelson 1969; Fitch 1970, 1985; Gregory 1975, 1977, 1982; Gordon and Cook 1980; Semlitsch and Moran 1984; Saint Girons 1985; Seigel and Ford 1987; Brodie and Ducey 1989; Ford et al. 1990; Brown 1992; Shine and Seigel 1996; Velhagen and Savitsky 1998); **ecology** (Blanchard 1937; Semlitsch and Moran 1984), **populations** (Lang 1969, Blanchard et al. 1979, Ford et al. 1991, Amaral 1999), **sex ratios** (Forbes 1940, Seibert and Hagen 1947), **conservation status** (Christansen 1981, Frank and Ramus 1994), **daily activity cycle** (Bider 1968), **annual activity cycle** (Goin and Goin 1953, Gibbons and Semlitsch 1987), **thermal ecology** (Brattstrom 1965, Brown et al. 1974, Amaral 1994), **habitat** (Barbour 1952, Heatwole and Getz 1960, Brummer 1985), **hibernation** (Criddle 1937, Lachner 1942, Neill 1948, Carpenter 1953, Bothner 1963, Lang 1969, Parker and Brown 1973, Brown et al. 1974, Gregory 1982), **ant hill occupancy** (Criddle 1937), **predation** (Medsger 1922, Harriot 1940, Wilson and Friddle 1946, Swanson 1952, Busack 1960, Puckette 1962, Wistrand 1972, Jackson and Franz 1981, Greene 1984, Knapik and Hodgson 1986, Barrett and Villarroul 1994); **defense behavior** (Gosner 1942, Axtell 1949, Warburton 1951, Jordon 1970, Carpenter and Ferguson 1977, Greene 1988, Watermolen 1991, Amaral 1999), **economic importance** (Pope 1937), **parasites** (Stiles and Hassell 1894, Guberlet 1928, Harwood 1932, Baker 1978), **arboviruses** (Whiting et al. 1968, Hoff and Trainer 1973), **poisoning** (Sights 1949), **movements** (Lang 1969), **diet and feeding behavior** (Schmidt and Inger 1957; Barbour 1950; Hamilton and Pollack 1956; Brown 1979a, 1979b; Johnson 2000; Rossman and Myer 1990; Amaral 1994; Ducey et al. 1999), **color morphs and albinos** (Loennberg 1894, Spencer 1915, Hensley 1959, Neill 1963, Grudzien and Owens 1991), **longevity** (Conant and Hudson 1949, Snider and Bowler 1992), **husbandry** (Rossi 1992), and **bibliography** (Dixon 1987).

• **REMARKS.** Holbrook (1842) considered *Coluber leberis* Linnaeus 1758 a senior synonym of *Tropidonotus septemvittata* (= *Regina septemvittata*) (Say 1825), but Boulenger (1893) rejected this and placed the name in the synonomy of *Heterodon platyrhinos* with a question mark. Klauber (1948) and Smith and Huheey (1960) showed that the description supplied by Linnaeus more properly matched that of *Coluber occipitomaculata* (= *Storeria occipitomaculata*) Storer 1839 than *R. septemvittata*, and rejected its assignment to that species. Smith and Huheey (1960) thought the 110 ventrals and 50 subcaudals given by Linnaeus were too low for *R. septemvittata*, but within the ranges of these scales in *S. occipitomaculata*. The type locality, "Canada," does not distinguish between the two species, as both occur there, and the holotype of *Coluber leberis* is not known to exist and cannot provide further help in determining which species Linnaeus meant. Although *Coluber leberis* Linnaeus 1758 has precedence over *Coluber occipito-maculata* Storer 1839, it has not been used for this species since 1758, and constitutes a *nomen oblitum*.

Storeria hidalgoensis Taylor 1942 was considered a subspecies of *S. occipitomaculata* by Trapido (1944). It is found only at high altitudes in the Sierra Madre Orientale in México from Hidalgo north through eastern San Luis Potosí to Nuevo Léon. It is separated by over 600 km from the nearest locality of *S. occipitomaculata* in Texas, and was considered a full species by Flores-Villela (1993).

• **ETYMOLOGY.** The name *occipitomaculata* is derived from the Latin *occipit* meaning "back of the head or skull," and *maculata*, meaning "spotted," in reference to the pale markings on the nape that are found in some individuals of this taxon. The name *obscura* is from the Latin *obscurus*, meaning obscured or dusky. The name *pahasapae* is the Native American Sioux tribe name for the Black Hills of western South Dakota

and adjacent Wyoming, in reference to the area of occurrence of this taxon.

1. *Storeria occipitomaculata occipitomaculata* (Storer) Northern Red-bellied Snake

Coluber occipito-maculatus Storer 1839:230. See species synonomy.
Coluber venustus Hallowell 1847:278. See species synonomy.
Storeria occipito-maculata occipito-maculata: Trapido 1944:20.
Storeria occipitomaculata occipitomaculata: Schmidt 1953:166. First use of combination.

• **DEFINITION.** This subspecies of *Storeria occipitomaculata* has a pinkish to red venter, pale neck marks usually separated from the venter, fewer than 49 subcaudals in males and 42 in females, and normally no fusion of the ocular scales.

• **COMMENT.** *Storeria o. occipitomaculata* ranges from Nova Scotia westward to southeastern Saskatchewan and south to South Carolina and northern Georgia west to eastern Kansas and eastern Oklahoma. It integrades with *S. o. pahasapae* over a broad front in Saskatchewan, Manitoba, eastern North Dakota, eastern South Dakota, Minnesota, northwestern Iowa, and possibly western Kansas; and with *S. o. obscura* in the eastern Carolinas, northern Georgia, eastern Alabama, northern Mississippi, and southeastern Oklahoma (Ernst 1974, Conant and Collins 1998).

2. *Storeria occipitomaculata obscura* Trapido Florida Red-bellied Snake

Storeria occipito-maculata obscura Trapido 1944:33. Type locality, "Florida, Alachua County, Gainesville." Holotype, Field Museum of Natural History 8561, adult female, collected in October 1922 by T. Van Hyning (examined by author).

• **DEFINITION.** This subspecies of *Storeria occipitomaculata* has a yellow, orange or tan venter, lateral neck blotches extending to the venter, more than 53 subcaudals in males and 45 or more in females, and usually no fusion of the ocular scales.

• **COMMENT.** *Storeria occipitomaculata obscura* ranges from northern Florida and southern Georgia west across the Gulf Coastal Plain to southern Arkansas, Louisiana, eastern Texas, and southeastern Oklahoma.

3. *Storeria occipitomaculata pahasapae* Smith Black Hills Red-bellied Snake

Storeria occipitomaculata pahasapae Smith 1963:17. Type locality, "Dunmire's Lodge, Lead, Lawrence Co., South Dakota." Holotype, University of Illinois Museum of Natural History 48564, collected 16 August 1960 by Hobart M. Smith (not examined by author).

• **DEFINITION.** This subspecies of *Storeria occipitomaculata* has small neck blotches with the lateral ones either faint or absent, no more than 54 subcaudals and 117 ventrals in males and 47 or fewer subcaudals and a maximum of 124 ventrals in females, and often fusion of the ocular scales to present a 2–1 pattern of two preoculars and one postocular.

• **COMMENT.** *Storeria occipitomaculata pahasapae* is found in the Black Hills of extreme western South Dakota and adjacent eastern Wyoming, and in southeastern Saskatchewan, southern Manitoba, eastern North Dakota, eastern South Dakota, Minnesota, northwestern Iowa, possibly western Kansas, and southcentral Nebraska. As currently interpreted (Ernst 1974, Conant and Collins 1998), its range east of the Great Plains consists of a broad zone of intergradation with *S. o. occipitomaculata*. However, it is possible that this area instead represents a west to east cline in the characters of *S. o. pahasapae*. A latidudinal study across Minnesota and Wisconsin would help determine this.

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